6. THE LIFE CYCLE OF THE COLEOPTERA (Including the Strepsiptera).

Royal N. Chapman, University of Minnesota.

The magnitude of variations in the life cycle and form changes which are met with when the Coleoptera and the Strepsiptera are considered as a group are hardly exceeded by any other group of insects. When we remember that there are now considered to be more than one hundred families of Coleoptera containing, in all, over one hundred and fifty thousand species, it is not surprising that there is a great amount of variation.

Some of the standard works on the Coleoptera might lead one to believe that beetles have no larval or pupal stages, for they are not mentioned. When Buetenmuller published his catalogue of the described transformations in 1891, the eggs had been described for 52 species, the larvæ for 368, and the pupæ for 96 species in North America. While a considerable amount of progress has been made since that time it has been only during recent years that attempts have been made to correlate the knowledge of the transformations of even the smaller groups.

It is difficult to obtain accurate information with regard to the various life cycles, especially with regard to the conditions which cause variations in the duration of the various stages. The data on which this paper is based have been taken in part from statements in literature which seem to be dependable, and in part from original experimental evidence.

The type forms of the various stages of the life cycle are subject to great variation throughout the group. The majority of the eggs are laid singly and unprotected, but the hydrophylid eggs are in covered cases and some of the Carabidæ deposit their eggs in cases constructed of mud. The egg stage is eliminated among at least some of the Strepsiptera which are viviparous.

The commonest larval form is campodiform or eruciform, being elongate and possessing thoracic legs, but all types of larvæ are represented. The generalized carabid larvæ are

typically campodiform, some of the Tenebrionidæ may be taken for the eruciform, while certain of the Buprestidæ, Cerambycidæ, Ipidæ and others represent the apodiform type.

The metamorphosis is complete, but there are cases of hypermetamorphosis. Among the Meloidæ we have this specialized type of development which illustrates, in a single species, all three types of larvæ, the campodiform, the eruciform (perhaps more scarabeoid) and the apodiform. There are other changes of form from one instar to another in the case of *Taphrocerus* (Buprestidæ) which hatches with the structure of a typical wood borer, but which appears later with the structure of a typical leaf miner. Some of the Bruchidæ have small functional thoracic legs in the first instar, but after they enter the nutrient substance in which the remainder of their life is to be spent, they become apodiform.

The pupæ are usually soft and protected from evaporation by a cell formed from materials of the environment cemented together by a secretion. However, some of the leaf miners which pupate in the leaves where the thin epidermis gives them little protection (*Taphrocerus*, Buprestidæ) are covered with a coat of chitin.

Most adult beetles are similar in general form, but the Platypsyllidæ are parasitic upon beavers and resemble other parasites which live upon vertebrate hosts. Indeed they were first described as Mallophaga. Specialization has led to degeneration in the case of the rhipaphorid parasite of the cockroach, the female of which is larviform. Among the Strepsiptera there are cases which have gone much farther and the female is a sack-like organism without means of locomotion which remains attached to its host throughout its life and from which the young emerge as larvæ.

The number of broods, the length of life and the number of molts are of the greatest significance in this consideration. These are interdependent and inseperable. There is no great uniformity in these respects when the group is considered as a whole nor is there always constancy even within a single species. Changes in certain environmental factors may alter the number of broods, change the length of life and the number of molts. But it should not be concluded that a change in a certain factor will cause a change in all species, or that some species can be changed at all. Nor are we justified in concluding, a priori,

that even the inherent tendencies toward periodicity may not be altered. In general those forms which are found in more or less uniform environmental conditions respond most readily to changes of the environment. Examples of this may be found among the beetles which live in stored food products. On the other hand, the beetles which feel the effects of the periodic changes of the season, having their food available for a limited period of each year, often have developed a periodicity with regard to their life phenomena.

Tribolium confusum has its egg stage shortened from ten to five days by a rise of from 24° to 34°, and it will develop one generation after the other throughout the year. On the other hand, the life cycle may be prolonged by a reduction of the amount of moisture and also by a limitation of the quantity or quality of the food. Thus the length of life and the number of broods may be altered by changing any one or all of these three factors. A larva now under observation has had its life prolonged from thirty to ninety days due to food conditions, and during this time it has molted twelve times rather than the normal six times.

So far as is known, all beetles have their lives shortened by an increase of temperature, over that which they normally experience. But some of them will not produce more broods in a year under high temperature than under low. The cotton boll weevil, a native of the south, has been reported to have as many broods a year as time, temperature, and humidity will allow, but the potato beetle always has two broods a year. Those forms which are not subject to an inherent periodicity have more broods in the south than in the north, but those with a fixed periodicity cannot be so changed. Shelford reports that a certain cicindelid has the last larval instar prolonged to extend over the period of hibernation in Canada, while the same species has a shorter larval life in the vicinity of Chicago.

The Buprestidæ as a family hibernate in the larval stage, but *Taphrocerus* which mines in the leaves of the floodplain bullrush as a larva, emerges and hibernates in the adult stage. In this case the larval life is confined to about six weeks in the early part of the summer and the adult beetles emerge and feed about on the leaves, but no eggs are deposited until the following spring. On the other hand, the larvæ of *Agrilus bilineatus*, a wood-boring buprestid, may mature in August and form their

pupal cells, in which they will remain as larvæ until the following spring, even though the temperature rises during September and there is ample time for them to transform and emerge as adult beetles. However, there would not be time for the eggs to be deposited and hatched and for the larvæ of the next generation to penetrate the bark of the tree before winter.

Among some of the Staphylinidæ which are reported as being symbiotic with ants, the larval life is said to be only fourteen days. On the other hand there are cases reported in which certain of the Cerambycidæ have been known to live as larvæ for years in dry wood.

If a statement were to be made with regard to the usual length of the egg stage of the Coleoptera as a whole, it would probably be to the effect that the egg stage is normally ten days in length. The Staphylinidæ already referred to as being symbiotic with ants, have an egg stage which is said to be of only two days duration. Still others of this same family have no egg stage at all. Several species of the Chrysomelidæ and the Strepsiptera are also viviparous.

The adult life is no more constant throughout the group than the other stages are. The adult life of many beetles coincides roughly with the growing season, although some of the Carabidæ have been observed to live for more than a year. Adults of the genus *Tribolium* have been kept for more than a year at room temperature and oviposition continued throughout this period. The males of some of the Strepsiptera are reported as living but fifteen or twenty minutes of extremely active life, while the females, in the absence of the egg stage, must live a more prolonged life in order that the young may develop within them.

The larvæ molt their skins in a more or less periodic way. Five or six instars may be considered as common, but among some of the Buprestidæ and others the number of molts may be increased when the larval life is prolonged as a result of unfavorable environmental conditions. One of the Tenebrionidæ has already been referred to as having had its life prolonged to three times the normal period during which time it has molted twice the normal number of times.

To turn to the consideration of the significance of these facts in relation to the environment it is necessary to avoid being lost in a vast amount of detailed information. In this

limited space it is possible to make only a few generalizations. A precaution may well be taken with regard to the use of the word "adaptation." In the minds of some of the modern biologists it is not orthodox to even mention this word. Therefore this word will not be used, but attention is called to the fact that the insects of this vast group are fitted into the environment wherever they will fit, with the result that certain type forms, together with certain biological characteristics, are to be found in the different types of environment.

There is a considerable group of aquatic beetles. Some of the larvæ crawl about over the submerged vegetation and resemble some of the neuropteroid larvæ of the same habitat as much as they do other closely related Coleoptera. In the swift water of a lotic environment the limpet-like larva of *Sphenus* is to be found.

A large group of beetles typified by the Carabidæ is found on the ground and under its cover of debris. The campodiform type of these larvæ has already been referred to and it is to be noted that this same type form is to be found among all surface feeding larvæ whether they feed upon the ground as the Carabidæ do or whether they are slightly modified for feeding upon the surface of plants as the Chrysomelidæ and Coccinellidæ do. These type forms, however, are characteristic of the families only in so far as the species retain the typical habits of the families. The family Chrysomelidæ has certain members which feed upon aquatic plants and these species have departed from the family type and have taken on various specializations leading to a virtual apodiform condition in some species.

Another great group of beetles passes the larval life within the nutrient medium. Some of these make their way through a hard substance with a great deal of effort and are typically apodiform. They are highly specialized for this mode of life and are helpless upon an exposed surface. Others which are normally found in softer substances may have well developed thoracic legs, as in cases where it is necessary for the larvæ to pass through a large amount of substance in order to accumulate enough nutrient material for maintenance and growth. Still others which live in a soft medium of high nutrient value may have limited means of locomotion and the entire larval life may be spent in a very limited space.

The more complicated life cycles have the most extreme changes of form connected with them, such as have been referred to in connection with the form changes of the larvæ. The Meloidæ are the best examples of this specialization, including such examples as *Epicauta*, the larva of which is at first campodiform and free living, but after it has located the egg pod of one of the Orthoptera, it enters into an arcuate larva with greatly reduced thoracic legs. Thus we have in a single life cycle a combination of the free living and restricted habits of life and they are accompanied by the typical larval forms which are to be correlated with them.

The impress of climate on the life cycle of the beetle is unmistakable. However, the effect of temperature upon the length of the various stages has already been referred to in connection with the length of life cycle and will not be discussed further.

Food is a factor which, like climatic conditions, may alter the length of the cycle as a whole or certain stages of it. This factor has been greatly neglected and a better understanding of it will undoubtedly be a great aid in bringing order out of the confusing detail which is to be met with in studying the biology of the Coleoptera.

The herbivorous beetles which are dependent upon growing plant tissue for their food may be said to have the factors of food and climatic conditions more or less merged into one. Conditions which favor the growth of plants favor the food supply, and thus control the growth and development of the beetles.

Beetles which live within their nutrient medium may be in the leaves of plants, in the fruiting bodies, or they may be in the supporting structures such as wood. These forms lend themselves to experimentation, for it is possible to correlate their rate of growth with the nutrient value of the material in which they live. The wood boring forms are notoriously long lived and the leafminers are usually short lived. Here with conditions of temperature and humidity constant it is possible to prolong or shorten the life cycle by controlling the nutrient value of the food.

The relatively simple condition just cited merges into a more complicated condition met with in the forms which are termed scavengers. While these forms appear to be subsisting upon

dead plant and animal matter, this material is teeming with life. The basic processes of amonification, nitrogen fixation, and the synthesis of proteins are being carried on by these micro-organisms and the beetle which feeds upon this decaying matter profits by their activity. It has been shown, in the case of some insects, that under certain conditions the rate of growth is in direct proportion to the number of micro organisms in the food.

One has but to review the food lists of the beetles to note in how many cases they are known to feed upon fungi or upon substances which may well contain micro organisms. When this subject has been investigated further we may come to a newer and more rational undertsanding of the life cycle of the Coleoptera.

---

7. THE LIFE CYCLE OF THE DIPTERA.

C. L. Metcalf, Ohio State University.

In attempting a summary such as this, one is almost dismayed by the great gaps in our knowledge of even the commonest species. Doubtless many of the gaps in what follows could be filled by a more careful scrutiny of the literature; many more, I am sure, could be filled from unpublished records and observations of the members of this Society; but when all this is recorded we shall find that very much more investigation must be performed before we can so much as give a comprehensive statement for all the species of a single family or for a single species of each family.

I do not believe that the order Diptera is surpassed, either within or without the class Insecta, for variety of habits and complexity of bionomics; and it seems to me an impossible task to present in a brief paper anything like a satisfactory picture of the life-cycle of the flies.

Not only is data wanting for more than a fraction of a per cent of the species; but, moreover, in the families where our knowledge is more complete, the most impressive thing is that *there is no agreement or uniformity of habit.* Where uniformity appears in my statements it is possibly because we know only a few of the many species in that group.